Fundamental theorem of natural selection under gene–culture transmission

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ABSTRACT A generalized fundamental theorem of natural selection is derived for populations incorporating both genetic and cultural transmission. The phenotype is determined by an arbitrary number of multiallelic loci with two-factor epistasis and an arbitrary linkage map, as well as by cultural transmission from the parents. Generations are discrete but partially overlapping, and mating may be nonrandom at either the genotypic or the phenotypic level (or both). I show that cultural transmission has several important implications for the evolution of population fitness, most notably that there is a time lag in the response to selection such that the future evolution depends on the past selection history of the population.

Fisher's fundamental theorem of natural selection (1) states that the rate of change in the average fitness of a population is proportional to the additive genetic variance in fitness. Since its original derivation, there have appeared a number of extensions of the theorem to multiple loci under generalized mating (2–7), as well as to the case of both fertility and viability selection (8–10). In all these models, fitnesses are assigned to genotypes, so that deterministic changes in the mean fitness arise solely from changes in the genetic composition of the population.

While these models are appropriate for some traits, they are not appropriate for traits subject to both genetic and cultural transmission. In the latter case, the probability of an individual's developing a particular phenotype depends on both his or her genetic constitution and the social environment in which he or she was raised. Consequently, it is the transmission of both genetic and cultural information [gene–culture transmission (11)] that determines how traits evolve. Given the prevalence of cultural transmission in both human (12, 13) and nonhuman (14) populations and the growing interest in the effects of cultural transmission on evolution (11, 15–18), there is a need to develop an analog of Fisher's theorem for the gene–culture case. My first attempt (19) considered the simple situation where fitness is determined by a single locus subject to random mating. In this note, the analysis is extended to the more realistic case of an arbitrary number of loci under generalized mating.

THE MODEL

Offspring are born and spend a period of time in the company of their parents. By the end of this socialization period, the offspring phenotype is fully developed and is fixed for the duration of the offspring's lifetime. In the case considered here, the phenotype is fitness, expressed as a survival probability to reproductive maturity. Juveniles that survive to reproductive maturity then mate to produce the next generation.

Suppose there are L loci and M_n alleles $A_{i_n}^{(n)}$ ($i_n = 1, 2, \ldots, M_n$) at locus n. Let $i = (i_1, i_2, \ldots, i_L)$ and $(i, j) = ((i_1, j_1), (i_2, j_2), \ldots, (i_L, j_L))$ and denote the frequency of haploid genotype (gamete) $A_{i_1}^{(1)} A_{i_2}^{(2)} \ldots A_{i_L}^{(L)} \equiv A_i$ by p_i and the frequency of the ordered diploid genotype among juveniles after socialization $A_{i_1}^{(1)} A_{j_1}^{(1)} / A_{i_2}^{(2)} A_{j_2}^{(2)} / \ldots / A_{i_L}^{(L)} A_{j_L}^{(L)} \equiv A_i A_j$ by P_{ij}. Let $\varphi_{ij}(x, y)dx\,dy$ be the proportion of juveniles after socialization but prior to reproduction with genotype $A_i A_j$ who have *parents* with fitness values in $[x, x + dx]$ and $[y, y + dy]$ [hereafter referred to as *genoparental type* $A_i A_j(x, y)$], and let $P_{ij}(z)dz$ be the proportion of juveniles with genotype $A_i A_j$ and fitness in $[z, z + dz]$. Let $W_{ij}(x, y)$ denote the average fitness of an individual with genotype $A_i A_j$ and parental values (x, y). The mean fitness of the population is then

$$\overline{W} = \sum_{ij} \int \int dx\,dy\; W_{ij}(x, y)\varphi_{ij}(x, y). \qquad [1]$$

In what follows, prime denotes values in the next generation and Δ denotes the per generation change. From Eq. 1, we have

$$\Delta \overline{W} = \overline{\Delta W} + \sum_{ij} \int \int dx\,dy\; W_{ij}(x, y)\Delta\varphi_{ij}(x, y) \qquad [2]$$

as the per generation change in the average fitness $\overline{W}$, where $\overline{\Delta W}$ is the mean of changes in the average fitness of individuals of specified genotype and parentage over the next generation:

$$\overline{\Delta W} = \sum_{ij} \int \int dx\,dy\; \Delta W_{ij}(x, y)\varphi_{ij}(x, y)'. \qquad [3]$$

We can decompose $W_{ij}(x, y)$ as

$$W_{ij}(x, y) = \overline{W} + w_{ij} + c(x, y) + \varepsilon_{ij}(x, y), \qquad [4]$$

with

$$c(x, y) = \beta_1(x) + \beta_2(y) + \eta(x, y). \qquad [5]$$

In Eq. 4, w_{ij}, $c(x, y)$ and $\varepsilon_{ij}(x, y)$ are genotypic, cultural, and gene–culture deviations quantifying the effect of genotype, parental phenotype, and the interaction of genotype and parental phenotype on offspring phenotype, respectively. In decomposing $W_{ij}(x, y)$ as shown, I assume that cultural transmission is from parents to offspring (12). I also assume that while an offspring's genotype may influence the probability of it developing a particular trait, all parental genotypes are equally effective at transmitting their phenotype. In Eq. 5, the cultural deviation is decomposed into additive contributions by each parent β_k and a cultural "dominance" term η.

To allow for nonrandom mating at both the genotypic and phenotypic levels, set

$$Q_{ij}(x, y) = \varphi_{ij}(x, y) - \varphi_i(x)\varphi_j(y), \qquad [6]$$

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where $\varphi_i(x)dx = \Sigma_j \int dy\ dx\varphi_{ij}(x, y)$ is the proportion of individuals with haploid genotype A_i and at least one parent with fitness in $[x, x + dx]$. $Q_{ij}(x, y)$ defines a gene–culture deviation from random mating. If there is random combination of gametes and random mating among parental phenotypes, $Q_{ij}(x, y) = 0$ for all i, j, x, and y. Integrating in Eq. 6 with respect to x and y, and summing over i and j give, respectively,

$$Q_{ij} = P_{ij} - p_i p_j, \qquad [7a]$$

$$Q(x, y) = \varphi(x, y) - \varphi(x)\varphi(y), \qquad [7b]$$

where Q_{ij} is the deviation from random combination of gametes, $Q(x, y)$ is the deviation from random combination of parental phenotypes, and $\varphi(y)dy = \Sigma_{ij} \int dx\ dy\ \varphi_{ij}(x, y)$ is the proportion of juveniles having at least one parent with phenotypic value in $[y, y + dy]$.

The per generation change in the mean fitness can be written as

$$\Delta\overline{W} = \overline{\Delta W} + \Delta\overline{W}_G + \Delta\overline{W}_C + \Delta\overline{W}_{GC}, \qquad [8]$$

where $\Delta\overline{W}_G$, $\Delta\overline{W}_C$, and $\Delta\overline{W}_{GC}$ are the components of change arising from genetic, cultural, and gene–culture effects, respectively. I suppose that the multilocus genotypic deviation w_{ij} can be decomposed as

$$w_{ij} = \sum_{m,n} w_{qr,kl}^{(m,n)}, \qquad q_m, r_n \in i; k_m, l_n \in j, \qquad [9]$$

i.e., as the sum of two-locus contributions $w_{qr,kl}^{(m,n)}$, where for ease of notation here and henceforth I suppress the double subscripts. Set

$$w_{qr,kl}^{(m,n)} = w_{qr}^{(m,n)} + w_{kl}^{(m,n)} + d_{qr,kl}^{(m,n)}, \qquad [10a]$$

$$w_{kl}^{(m,n)} = \alpha_k^{(m)} + \alpha_l^{(n)} + e_{kl}^{(m,n)}. \qquad [10b]$$

In Eq. 10a, the two-locus contribution is decomposed as the sum of two-locus gametic contributions $w_{qr}^{(m,n)}$ and $w_{kl}^{(m,n)}$ and a two-locus dominance deviation $d_{qr,kl}^{(m,n)}$, while in Eq. 10b the two-locus gametic contributions are in turn decomposed as the sum of allelic contributions at each locus ($\alpha_k^{(m)}$, $\alpha_l^{(n)}$) and a two-locus gametic epistatic deviation $e_{kl}^{(m,n)}$. Let $p_i^{(n)}$, $p_{ij}^{(m,n)}$, and $P_{ij,kl}^{(m,n)}$ be the frequency of allele $A_i^{(n)}$, the two-locus gamete $A_i^{(m)}A_j^{(n)}$, and the two-locus genotype $A_i^{(m)}A_j^{(n)}/A_k^{(m)}A_l^{(n)}$, respectively. Noting that

$$p_i^{(n)} = \sum_j^{(n)} p_j, \quad p_{ij}^{(m,n)} = \sum_k^{(m,n)} p_k, \quad P_{ij,kl}^{(m,n)} = \sum_{qr}^{(m,n)} P_{qr}, \qquad [11]$$

where the summations extend over all multilocus gametes carrying allele $A_i^{(n)}$, alleles $A_i^{(m)}$ and $A_j^{(n)}$, and over all multilocus genotypes with the two-locus genotype $A_i^{(m)}A_j^{(n)}/A_k^{(m)}A_l^{(n)}$, letting $r^{(m,n)}$ denote the recombination fraction between loci m and n, and setting $\xi_{ij}^{(m,n)}$ and $\xi_i^{(n)}$ as the average excess for fitness of gamete $A_i^{(m)}A_j^{(n)}$ and allele $A_i^{(n)}$, respectively, we get

$$\overline{W}\Delta p_{ij}^{(m,n)} = p_{ij}^{(m,n)}\xi_{ij}^{(m,n)} - r^{(m,n)} D_{ij}^{(m,n)}, \qquad [12a]$$

$$\overline{W}\Delta p_i^{(n)} = p_i^{(n)} \xi_i^{(n)} \qquad [12b]$$

(see ref. 20, pp. 92–93, and ref. 7, p. 1911, for the derivation of Eqs. 12a and 12b, respectively), where

$$D_{ij}^{(m,n)} = \sum_{k,l} (W_{ij,kl}^{(m,n)}p_{ij}^{(m,n)}p_{kl}^{(m,n)} - W_{il,kj}^{(m,n)} p_{il}^{(m,n)} p_{kj}^{(m,n)}) \qquad [13]$$

are the standard linkage disequilibria and $W_{ij,kl}^{(m,n)}$ is the average fitness of the two-locus genotype $A_i^{(m)}A_j^{(n)}/A_k^{(m)}A_l^{(n)}$. Setting

$$Q_{ij,kl}^{(m,n)} = P_{ij,kl}^{(m,n)} - p_{ij}^{(m,n)} p_{kl}^{(m,n)} \qquad [14]$$

as the deviation from random combination of gametes at loci m and n, noting that

$$\Delta\overline{W}_G = \sum_{ij} w_{ij}\Delta P_{ij}, \qquad [15]$$

recalling Eq. 7a and employing successively Eqs. 8–14 in Eq. 15, we eventually get

$$\Delta\overline{W}_G = \frac{V_g + V_e - 2A}{\overline{W}} + \frac{B - 2C + D}{\overline{W}^2} + E, \qquad [16]$$

as the genetic component of the per generation change in mean fitness, with

$$V_g = 2\sum_n \sum_i \alpha_i^{(n)} \xi_i^{(n)} p_i^{(n)}, \qquad [17a]$$

$$V_e = 2\sum_{m,n} \sum_{ij} e_{ij}^{(m,n)} \xi_{ij}^{(m,n)} p_{ij}^{(m,n)}, \qquad [17b]$$

$$A = \sum_{m,n} r^{(m,n)} \sum_{ij} e_{ij}^{(m,n)} D_{ij}^{(m,n)}, \qquad [17c]$$

$$B = \sum_{m,n} \sum_{qr,kl} d_{qr,kl}^{(m,n)} p_{qr}^{(m,n)} p_{kl}^{(m,n)} \xi_{qr}^{(m,n)} \xi_{kl}^{(m,n)}, \qquad [17d]$$

$$C = \sum_{m,n} r^{(m,n)} \sum_{qr,kl} d_{qr,kl}^{(m,n)} p_{kl}^{(m,n)} \xi_{kl}^{(m,n)} D_{qr}^{(m,n)}, \qquad [17e]$$

$$D = \sum_{m,n} r^{(m,n)2} \sum_{qr,kl} d_{qr,kl}^{(m,n)} D_{qr}^{(m,n)} D_{kl}^{(m,n)}, \qquad [17f]$$

$$E = \sum_{m,n} \sum_{qr,kl} d_{qr,kl}^{(m,n)} \Delta Q_{qr,kl}^{(m,n)}. \qquad [17g]$$

Eq. 16 is a generalization of Nagylaki's (5) two-locus result, with the E term added. In purely genetic systems, Hardy–Weinberg proportions obtain in a single generation, so at all subsequent times $E = 0$. However, in the biocultural case there will generally be some persistent element of nonrandom mating at the phenotypic level, and $E \neq 0$ in general.

Consider now $\Delta\overline{W}_C$:

$$\Delta\overline{W}_C = \int \int dx\ dy\ c(x, y)\Delta\varphi(x, y). \qquad [18]$$

If there are no differences in fertility, the proportion of offspring in the next generation having at least one parent with fitness in $[x, x + dx]$ is simply the proportion of juveniles in the previous generation with fitness in $[x, x + dx]$ that survive to reproductive maturity. So if $\phi(x) = \Sigma_{ij}P_{ij}(x)$ is the phenotype density among juveniles before selection, we have

$$\Delta\varphi(x) = \phi(x)^* - \varphi(x), \qquad [19]$$

where $\phi(x)^* = \phi(x)x/\overline{W}$ is the fitness density after selection in the parental generation. Recalling Eqs. 5 and 7b and substituting Eq. 19, we eventually obtain

$$\Delta\overline{W}_C = \frac{\overline{\beta w}}{\overline{W}} + \frac{\overline{\eta w^2}}{\overline{W}^2} + H, \qquad [20]$$

where

$$\overline{\beta w} = \sum_{k=1}^{2} \int dx\ \beta_k(x)x\phi(x), \qquad [21a]$$

$$\overline{\eta w^2} = \int \int dx \, dy \, \eta(x, y) xy \phi(x) \phi(y), \qquad [21\text{b}]$$

$$H = \int \int dx \, dy \, \eta(x, y) \Delta Q(x, y). \qquad [21\text{c}]$$

Finally, consider $\Delta \overline{W}_{GC}$ given by

$$\Delta \overline{W}_{GC} = \sum_{ij} \int \int dx \, dy \, \varepsilon_{ij}(x, y) \Delta \varphi_{ij}(x, y). \qquad [22]$$

Let $p_i(x) dx = \Sigma_j \, P_{ij}(x) dx$ be the density of juveniles before selection with haploid genotype A_i and fitness in $[x, x + dx]$. Assuming no fertility differences among genotypes or phenotypes,

$$\Delta \varphi_i(x) = p_i(x)^* - \varphi_i(x), \qquad [23]$$

where $p_i(x)^* = p_i(x) x / \overline{W}$ is the density of individuals with haploid genotype A_i and fitness in $[x, x + dx]$ after selection in the parental generation. Recalling Eq. 6, using Eq. 23, and noting that

$$\sum_j \int dy \, \varepsilon_{ij}(x, y) \varphi_j(y) = 0, \qquad [24]$$

yields

$$\Delta \overline{W}_{GC} = \frac{\overline{\varepsilon w^2}}{\overline{W}^2} + K, \qquad [25]$$

where

$$\overline{\varepsilon w^2} = \sum_{ij} \int \int dx \, dy \, \varepsilon_{ij}(x, y) xy \, p_i(x) p_j(y), \qquad [26\text{a}]$$

$$K = \sum_{ij} \int \int dx \, dy \, \varepsilon_{ij}(x, y) \Delta Q_{ij}(x, y). \qquad [26\text{b}]$$

Putting together Eqs. 16, 20, and 25, we finally obtain

$$\Delta \overline{W} = \overline{\Delta W} + \frac{1}{\overline{W}} (V_g + V_e + \overline{\beta w} - 2A)$$

$$+ \frac{1}{\overline{W}^2} (B - 2C + D + \overline{\eta w^2} + \overline{\varepsilon w^2}) + E + H + K \qquad [26]$$

as the per generation change in population fitness.

DISCUSSION

Eq. 26 represents a generalized fundamental theorem of natural selection under gene–culture transmission, of which the purely genetic scenario considered by Fisher and subsequent workers is a special case. For example, when there are no cultural effects $[c(x, y) = 0]$, no gene–culture effects $[\varepsilon_{ij}(x, y) = 0]$, and Hardy–Weinberg proportions obtain, Eq. 26 reduces to the multilocus generalization of Nagylaki (equation 70 of ref. 5) result

$$\Delta \overline{W} = \overline{\Delta W} + \frac{1}{\overline{W}} (V_g + V_e - 2A) + \frac{1}{\overline{W}^2} (B - 2C + D). \qquad [27]$$

Furthermore, if we assume constant genotypic fitness, no epistasis, no linkage, and weak selection, and we scale the genotypic fitnesses appropriately (see ref. 7), Eq. 25 further reduces approximately to Fisher's fundamental theorem $\Delta \overline{W} \approx V_g$.

Comparison of Eqs. 26 and 27 illustrates the effects of cultural transmission on the evolution of population fitness. It is apparent that under gene–culture transmission, mean fitness can continue to evolve even if the genetic (additive plus epistatic) variance in fitness has been exhausted. Moreover, even for the simple case of random mating, no epistasis, and constant fitnesses, fitness can decline (since $\overline{\beta w}$ may be negative), whereas in the genetic case under the same conditions, mean fitness is nondecreasing (7, 21).

There is one other important difference, namely, that cultural transmission introduces a time lag in the response of the population to selection. To see this, let t denote the generation number. Then $\varphi(x)_{t+1} = \phi(x)_t^*$ and $\Delta \varphi(x)_{t, t+1} = \phi(x)_t^* - \phi(x)_{t-1}^*$, so that the change in the density $\varphi(x)$ depends on selection in both the current and the previous generation. By contrast, in purely genetic systems, change depends only on selection in the current generation. This means that under gene–culture transmission, traits can continue to evolve after selection is relaxed (16–18), a phenomenon Kirkpatrick and Lande (18) have referred to as "evolutionary momentum."

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